HYBRIDS AND THEIR UTILIZATION IN PLANT BREEDING.

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INTRODUCTION.

Probably no question is of so much interest and importance to farmers and gardeners as the improvement of cultivated plants. Since the time of von Mons and Knight, the early part of the present century, this phase of plant culture has received considerable attention, but probably much less than it deserves. The experience of gardeners the world over has shown clearly that the possibilities in the improvement of our useful plants are almost unlimited. In the words of H. L. de Vilmorin, "No limit can be fixed as to the improvements which may be expected from care, thought, and selection. The gains of the last dozen years may surely be taken as the forerunners of better things." The last half century has witnessed unprecedented extensions of the areas devoted to agriculture, and this has led to a demand, still imperfectly satisfied, for new sorts of cultivated plants adapted to the particular conditions of climate and soil in each new region.

The great variety of soil and climatic conditions which this country affords renders it necessary to have many sorts of cultivated plants differing in their requirements. For instance, a tomato of the greatest worth for growth in the State of New York may be totally unfit for general culture in Florida, and the same is true in the case of almost all cultivated plants. The sorts cultivated in New York are almost wholly different from those cultivated in the South and the West.

The revolution in methods of transportation effected during the present century has multiplied many fold the areas which can be devoted to intensive forms of agriculture, such as fruit growing, market gardening, floriculture, etc., and the increasing aggregation of population in cities has led to a much greater demand for such products. These causes have also brought about an unceasing demand for sorts of superlative excellence which will warrant the expense and trouble of the most intensive culture.

Again, the maximum productiveness in most of our cultivated plants has not been reached, and much can still be gained in this direction. In striving to produce improved sorts, the size and shape of fruit or seed, color, quality, and a host of other features must also be taken into account.

Doubtless many exceedingly valuable sorts remain to be introduced from other parts of the world, but even here the art of the plant breeder will in the end be necessary to secure in these plants variations particularly adapted to the new conditions to which they are exposed when removed from the regions where they originated.

In breeding plants two methods are commonly relied upon: (1) Variations arising naturally, supposed to be induced directly or indirectly by environment; and, (2) variations induced by crossing different varieties, species, or even genera. The first of these methods was discussed by one of the writers in the Yearbook of the Department for 1896, pp. 89–106, and the second will be considered here.

Inasmuch as the sexuality of plants was unknown, or at least very imperfectly understood, prior to the last two centuries, while a knowledge of the sex distinction of animals dates from the dawn of human history, it is not surprising that while the hybridizing of animals was well understood by the ancients they did not know that crossing was possible with plants. Experimental proof of the sexuality of plants was published for the first time by Camerarius, December 28, 1691, and only after this discovery was the function of pollen and its necessity for seed formation understood. About twenty years later Thomas Fairchild, an English gardener, made the first recognized plant hybrid by crossing the carnation with the sweet william. (Pl. XVII shows a hybrid carnation.) The plants grown from the hybridized seeds, known as Fairchild's sweet william, were cultivated at least a hundred years under the same name, and possibly are still in cultivation. The first careful studies of hybrid plants were made by Koelreuter in 1760, and not till nearly the middle of this century was his work surpassed.

In general, hybrids can be produced only between obviously related plants. With some plants, such as oaks and verbenas, hybrids are not of uncommon occurrence in nature, while with many others, indeed in the majority of cases, no spontaneous hybrids are known. Among plants which have been cultivated for a considerable period, however, it is not unusual for closely related species to cross, and the same is true even in certain species distinct enough to be classed in different genera, the latter forming the so-called bigeneric hybrids.

What can be accomplished by close application to the work of plant breeding is shown by the extraordinary results obtained in this country by Burbank and Munson; indeed, no feature of agricultural, horticultural, or floricultural work is more fascinating or more promising of valuable results.

WHAT ARE HYBRIDS?

The term hybrid is by many applied only to the offspring obtained by crossing two plants or animals sufficiently different to be considered by naturalists as distinct species, while the terms mongrel and cross

A Hoen & Co. Lith.

HYBRID CARNATION.

1. SCOTT, FEMALE PARENT. 3. HYBRID. 2. McGOWAN, MALE PARENT.

are used to designate the offspring of two races or varieties of one species. It was formerly supposed that all hybrids were more or less sterile, in contradistinction to mongrels, which were believed to be very fertile. It has been found, however, that many hybrids, in the narrow sense, are very fertile, and that some mongrels are nearly sterile. Since it is impossible to indicate by any two words, such as hybrid or mongrel, the various degrees of difference of the forms crossed, the word hybrid is here used, comformably to the Century Dictionary, as a generic term, to include all organisms arising from a cross of two forms noticeably different, whether the difference be great or slight. Adjectives are sometimes used to indicate the grade of the forms crossed, such as racial hybrid, bigeneric hybrid, etc. Where a hybrid of two species is crossed with a third species, a trispecific hybrid results.

The offspring produced by the union of two plants identical in kind, but separated in descent by at least several seed generations, is often called a crossed, cross-fertilized, or cross-bred plant, but it is not a hybrid, as the essential character of a hybrid is that it results from the union of plants differing more or less in kind, or, in other words, is the result of a union between different races, varieties, species, genera, etc. On the other hand, flowers impregnated with their own pollen, with the pollen of another flower on the same plant, or even with pollen from another plant derived from the same original stock by cuttings, grafts, etc., are said to be self-fertilized, and the offspring resulting from such unions are also termed self-fertilized plants. With some plants, such as tobacco and wheat, self-fertilization is the rule. In many cases, however, the flowers are so constructed that cross-fertilization is favored, as in corn, rye, etc., and in some cases cross-fertilization is necessary, all possibility of self-pollination being precluded, as in the case of hemp and other plants having the male and female flowers on separate individuals.

METHODS USED IN HYBRIDIZING PLANTS.

The process of hybridizing plants is in itself neither difficult nor mysterious, it being simply necessary to understand the general structure of the flower to be used. The flowers of tomato, pear, and orange may be taken as illustrating the common forms, although, of course, very many modifications occur. The envelopes of these flowers, as in the case of the flowers of most cultivated plants, consist of two whorls of modified leaves (figs. 3 and 5). The outer whorl, which is known as the calyx, is commonly green like the foliage and is divided into several distinct or more or less united lobes or sepals (figs. 3 and 5, *cx*), while the inner whorl, or corolla, is usually of some bright color other than green, and its different divisions or lobes are known as petals (figs. 3 and 5, *c*). In some cases, as in the lily, the calyx and corolla are of the same color, so that they are not easily distinguishable; while in still other cases, as in oaks, walnuts, etc., the corolla is entirely wanting.

The essential, or sexual, organs of the flower, the stamens and pistils, are found inside the calyx and corolla, and it is with these organs that the hybridizer is most concerned. The stamens, or male

FIG. 2.—Newly opened bud of Lorillard tomato, showing stage in which flower should be emasculated. (Natural size.)

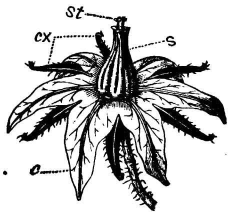

FIG. 3.—Mature flower of Lorillard tomato: *cx*, calyx; *c*, corolla; *s*, stamens; *st*, stigma. (Natural size.)

FIG. 4.—A flower of Lorillard tomato emasculated ready for pollination. (Natural size.)

organs, of the plant (figs. 3 and 5, *s*) are usually several in number, and are composed of an upper swollen portion, the anther, which is borne on a more or less slender stalk called the filament. In some flowers, as in those of the tomato, the filament is very short (figs. 3 and 5), and in others is entirely wanting, the anthers being borne at the base of the corolla. The very numerous small, yellow, powdery grains of pollen, which constitute the male fecundating elements, are borne in sacks in the anthers. When the anther matures these sacks burst open and the pollen is exposed. A quantity of this pollen must be transferred, either by natural or artificial means, to the stigma of the female organ in order to insure fecundation. The application of pollen to the stigma is designated pollination, and successful pollination—that is, the application of pollen to the stigma, followed by f e c u n d a t i o n—is termed fertilization.

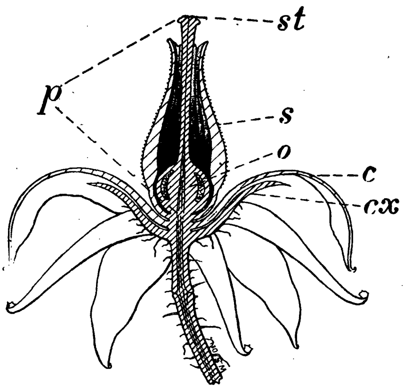

FIG. 5.—Section of a tomato flower: *cx*, calyx; *c*, corolla; *s*, stamens; *p*, pistil; *o*, ovary; *st*, stigma. (Twice natural size.)

The pistil or pistils (fig. 5, *p*), which are the female organs, occupy the center of the flower and are surrounded by the stamens. The upper portion of the pistil is usually somewhat swollen and more or less rough. It is on this portion of the pistil, known as the stigma (figs. 3 and 5, *st*), that the pollen must fall to produce fecundation.

In the majority of plants the stamens and pistils are produced in the same flower, as in the tomato and orange (figs. 3 and 7); but in certain plants they are produced in different flowers on the same plant, as in walnuts, castor beans, etc., or on different plants, as in the willow, poplar, etc.

In undertaking to hybridize plants artificially, it is well to remember that in many plants the stamens and pistils when in the same flower mature at different times—a provision to insure cross-pollination (the application of the pollen of one flower to the stigma of another). In a large majority of such cases the stamens ripen first, discharging their pollen before the pistil is receptive. The most important feature in the work of crossing is to exclude from the stigma all pollen except that which it is desired to use. As Darwin says, in reference to the breeding of animals, "The prevention of free crossing and the intentional matching of individual animals are the corner stones of the breeder's art." The prevention of self-pollination (the transfer of pollen to the stigma of the same flower) in perfect flowers, that is, flowers containing both stamens and pistils, necessitates the careful opening of the flowers intended for hybridi-

FIG. 6.—Orange flower bud, showing stage which should be selected for emasculation. (Natural size.)

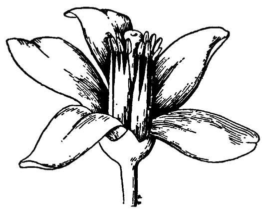

FIG. 7.—Mature orange flower. (Natural size.)

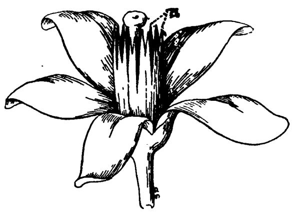

FIG. 8.—An emasculated orange flower: *a*, shows where anthers were detached. (Natural size.)

zation while they are still immature, and the cutting or pulling off of the anthers before they burst and allow the escape of the pollen. This process is termed emasculation. In the tomato the stamens and pistils do not mature until after the calyx and corolla become partially expanded. In this case the stamens should be cut off near the base (fig. 4) with a small pair of scissors shortly after the bud opens (fig. 2), a process which is in this case somewhat difficult.

In the manipulation of orange flowers mature buds nearly ready to open are selected (fig. 6), and the tips of the corolla carefully pried apart until the stamens are exposed. In these flowers the anthers are attached to the filaments by very slender threads, which are easily broken (fig. 7), so that the simplest method of removing the stamens is to pull them off with fine-pointed forceps. The latter may also be conveniently used in prying apart the corolla lobes of the bud. During the process of emasculation in this and all other cases great care must be exercised not to open the stamens and accidentally pollinate the flower. All insects must be watched and carefully excluded. Fig. 8 shows an emasculated flower ready to bag.

After emasculating the flower a bag of some closely woven cloth or of paper should be carefully passed over the twig bearing the flower and tied around the stem below the flower in such a manner as to effectually exclude all insects and foreign pollen (Pl. XVIII, fig. 1). The manila paper sacks used by grocers are employed almost exclusively for this purpose. In a few days after emasculation and bagging, when the pistils have had time to mature, the sacks must be removed and the pistils pollinated, after which the sacks should be replaced as before and allowed to remain until fecundation has taken place and all danger from the action of foreign pollen is over. In most cases the sacks should then be removed, as they are likely to injure the development of the fruit. In some cases, as in the orange, where the pistil is nearly mature when the bud is opened, the pollen may be applied to the stigma when the flower is emasculated, thus avoiding the trouble of opening the bag later. The flowers selected for emasculation and hybridization should be full-sized, perfect in all respects, and conveniently situated. Those on the end of a twig frequently set fruit best. All the flowers on the branch which are not used should be cut off. Frequently several flowers of the same age can be selected on the same branch, emasculated, and inclosed under the same bag.

In hybridizing, many different methods are followed in applying the pollen. In most cases where an abundance of pollen can be secured the freshly burst anthers from one plant may be taken with fine-pointed forceps and rubbed over the stigma of the other until sufficient pollen has been transferred. This is probably the easiest and safest method in most cases. Some hybridizers transfer the pollen with a small ladle or camel's-hair brush, and occasionally this method may be found somewhat convenient, especially where the pollen is brought from some distance and has largely escaped from the anthers.

After each pollination it is of the utmost importance to label the bag in such a way that there will be no question as to what it contains. These labels should be allowed to remain after the bag has been removed. As fruits like apples, oranges, etc., approach maturity it is very desirable that they be inclosed in gauze bags firmly tied to the branches (Pl. XVIII, fig. 2). Such bags allow the normal development of the fruit, protect it from being picked accidentally, and in case the fruit falls prematurely preserve it in connection with the label.

WHAT PLANTS CAN BE HYBRIDIZED?

It is a fact of prime importance that plants so different as to be classed by botanists in widely different families never yield offspring when crossed; for example, it is impossible to successfully cross Indian corn and lilies or the apple and walnut. Usually plants diverse

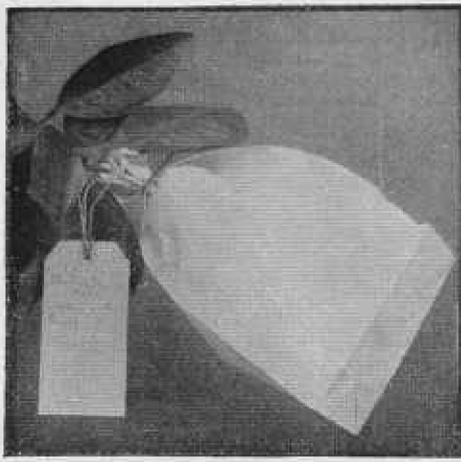

FIG. 1.—ORANGE FLOWER INCLOSED IN PAPER BAG AFTER EMASCULATION.

FIG. 2.—NEARLY MATURE HYBRID ORANGE INCLOSED IN GAUZE BAG TO PREVENT LOSS BY DROPPING.

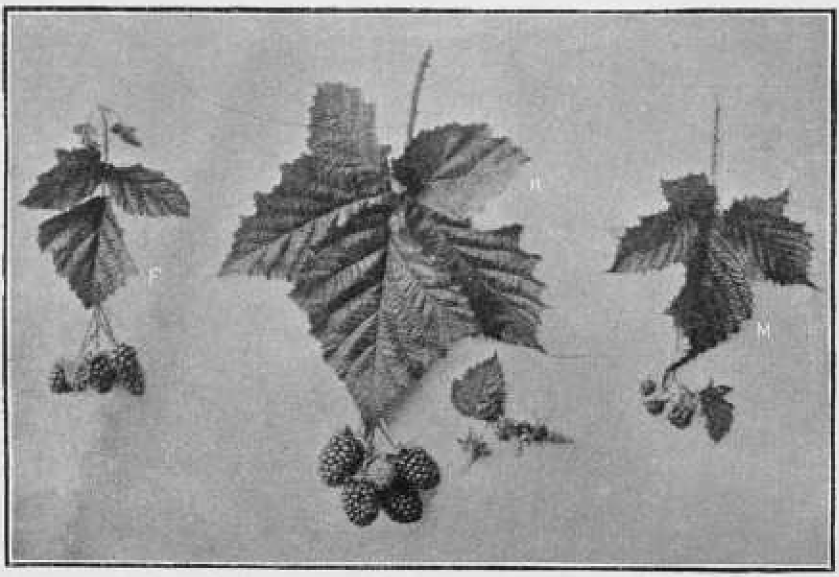

FIG. 3.—RASPBERRY-BLACKBERRY HYBRID "PRIMUS" AND PARENTS: F, CALIFORNIAN DEWBERRY (RUBUS URSINUS), FEMALE PARENT; H, HYBRID; M, SIBERIAN RASPBERRY (R. CRATÆGIFOLIUS), MALE PARENT (ABOUT ONE-FOURTH NATURAL SIZE). (AFTER BURBANK.)

FIG. 1.—CANES OF THE SECOND GENERATION OF A BLACKBERRY-RASPBERRY HYBRID, ALL GROWN FROM SEED OF ONE PLANT. (AFTER BURBANK.)

FIG. 2.—SEEDLING PINEAPPLES, THE OFFSPRING OF MORE THAN USUALLY SEEDLESS PLANTS RENDERED FERTILE BY POLLINATION WITH ANOTHER SORT: 5, EGYPTIAN QUEEN CROSSED WITH SMOOTH CAYENNE; 9, ENVILLE CITY CROSSED WITH SMOOTH CAYENNE; 21, ENVILLE CITY CROSSED WITH PUERTO RICO.

enough to be considered as belonging to clearly distinct genera, even though of the same natural family, are perfectly sterile when crossed; for example, Indian corn yields no offspring when cross-pollinated with wheat, nor does wheat when crossed with oats, although all belong to the great family of grasses. Plants belonging to the different cultivated races or to natural varieties of the same species are almost invariably fertile when crossed. Indeed, as will be shown later, they are sometimes more fertile when crossed with a related species than when fertilized by their own pollen. Different species of plants closely enough related to be placed in the same genus by naturalists are very often, though by no means always, capable of being hybridized.

Gaertner found that "one of the tobaccos, *Nicotiana acuminata*, which is not a particularly distinct species, obstinately failed to fertilize or to be fertilized by no less than eight species of Nicotiana." Darwin states that "in the same family there may be a genus, as Dianthus, in which very many species can most readily be crossed; and another genus, as Silene, in which the most persevering efforts have failed to produce between extremely close species a single hybrid." Again, there is considerable diversity in results in certain reciprocal crosses between the same two species. "*Mirabilis jalapa* can easily be fertilized by the pollen of *M. longiflora*, and the hybrids thus produced are sufficiently fertile; but Koelreuter tried more than two hundred times during eight following years to fertilize reciprocally *M. longiflora* with the pollen of *M. jalapa*, and utterly failed," as have also many other hybridizers. Frequently even very closely related species absolutely refuse to cross. According to Bailey and Pammel, this is true of the pumpkin (*Cucurbita pepo*) and squash (*C. maxima*). It is nevertheless true that hosts of very distinct species hybridize readily, and quite a number of cases are known where species belonging to different and quite distinct genera have hybridized, producing the so-called bigeneric hybrids. For instance, wheat and rye, and wheat and barley, belonging to closely related genera, cross with difficulty, and Luther Burbank has succeeded in obtaining a hybrid of strawberry and raspberry.

Focke cites the following instances of hybrids produced by crossing species belonging to different families: *Gladiolus blandus* Sol., belonging to the lily family, crossed with pollen of a species of Hippeastrum, belonging to the Amaryllis family, produced seed which yielded four plants. Again, six flowers of *Digitalis ambigua* Murr (Figwort family) when crossed by Campbell with the pollen of *Sinningia speciose* (Gloxinia family) gave three seed capsules, from which several plants were obtained. Hybrids between plants belonging to different families are, however, very rare. The results obtained by hosts of experimenters and practical gardeners show conclusively that the majority of closely related species can be readily crossed, while very distinct species and species belonging to distinct genera can be crossed in only comparatively few cases. It is impossible to predict what plants may or may not be hybridized.

In breeding cultivated varieties it has commonly been supposed that seedless plants, like the pineapple and navel orange, could not be utilized because of their seedlessness. The writers have found, however, that in each of these plants abundant seeds are produced when the flowers are crossed with pollen from distinct sorts (Pl. XIX, fig. 2). This suggests that fruits which are normally seedless may frequently be used to advantage in hybridizing experiments, particularly when it is desired to secure improved seedless varieties. For instance, a pomelo with few or no seeds might possibly be obtained by hybridizing the common pomelo with the navel orange.

HYBRIDS INTERMEDIATE BETWEEN THEIR PARENTS.

The characters of hybrids are almost always intermediate between the forms crossed, although sometimes they resemble one parent exclusively. As a rule, hybrids between distinct species are intermediate in the first generation and often exactly midway between their parents in all characters, while those between races or varieties of one species are variable in the first generation. Macfarlane has shown that not only do the hybrids he studied occupy a mean position as regards habit, size, shape of leaves, time of flowering, etc., but also in microscopic peculiarities of structure. For instance, the starch grains of *Hedychium gardnerianum* are small, flat, triangular plates, measuring from $\frac{10}{1000}$ to $\frac{12}{1000}$ of a millimeter from base to apex (fig. 9, *a*), and those of *H. coronarium* are ovate and measure from $\frac{32}{1000}$ to $\frac{60}{1000}$ of a millimeter in length (fig. 9, *b*), while in a hybrid of these two species known as *H. sadlerianum*, the starch grains are intermediate in size and shape (fig. 9, *h*). The thickened cells of the bundle sheath of the root of the so-called *Philageria veitchii*, a bigeneric hybrid (Pl. XX, fig. 3, *h*) are intermediate, not only in size and shape, but also in the number of laminations, between *Philesia buxifolia*, the male parent (Pl. XX, fig. 3, *m*), and *Lapageria rosea*, the female parent (Pl. XX, fig. 3, *f*). A skeletonized leaf of the same hybrid is shown on Pl. XX, fig. 4, *h*, in comparison with its parents (Pl. XX, fig. 4, *m* and *f*).

Other hybrids, though appearing strictly intermediate at first sight, are found on careful examination to possess, side by side, structures or organs characteristic of the parents and not intermediate between them; for instance, on the leaves of a hybrid of the gooseberry and black currant Macfarlane found the simple hairs of the former species and also the oil-secreting, shield-shaped hairs of the latter, though both were but half the size of those on the parents. In leaves of the York-Madeira grape, a hybrid of the summer grape (*Vitis æstivalis*) and the fox grape (*V. labrusca*), Millardet found sunken stomata, or breathing pores, like those in the former species, projecting ones like those in the latter, and many intermediate forms.

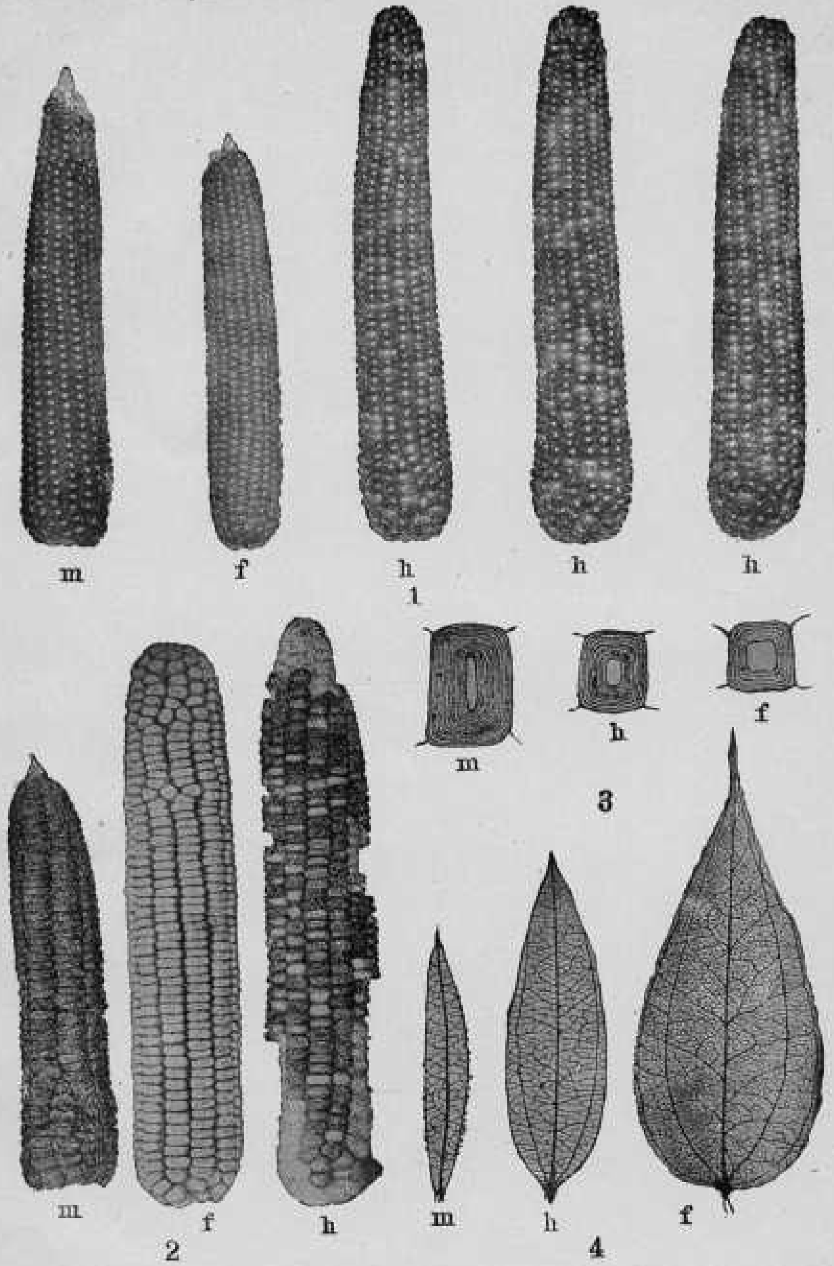

FIG. 1.—Indian corn, showing increase in size resulting from crossing different sorts: *m*, male parent, Queens Golden; *f*, female parent, common Pearl; *h h h*, cross-bred ears of first generatiou. (After McClure.)

FIG. 2.—Indian corn, showing immediate effect of foreign pollen: *m*, male parent, Black Mexican; *f*, female parent, White Dent; *h*, ear of White Deut pollinated with Black Mexican, showing immediate result of the cross. (After McClure.)

FIG. 3.—Bundle-sheath cells of roots of hybrid and parents, showing intermediate nature of hybrid: *m*, *Philesia buxifolia*, male parent; *h*, hybrid; *f*, *Lapageria rosea*, female parent. (After Macfarlane.)

FIG. 4.—Skeleton leaves of hybrid and parents, showing the intermediate character of hybrid: *m*, *Philesia buxifolia*, male parent; *h*, hybrid; *f*, *Lapageria rosea*, female parent. (After Macfarlane.)

Not infrequently the color of the flowers of a hybrid is not a uniform blend between those of the parents, but the two parental colors occur side by side in patches. This is exemplified by many of the hybrid carnations obtained by crossing Scott and McGowan. One of these hybrids, produced by Mr. E. C. Rittue, gardener of the Division of Vegetable Physiology and Pathology, is shown on Pl. XVII, fig. 3, though the bands of reddish color in this case are not exactly the same tint as the pink flowers of the male parent Scott. Strasburger has aptly said that in such cases "the hybrid is a sort of mosaic made up of portions of the two parents."

The hybrid may in rare instances show parts of considerable size resembling almost exactly similar parts of one of the parents, while other parts of the hybrid may show an equally striking resemblance to the other parent. Instances of this are furnished by some grape hybrids, as will be explained more in detail in speaking of some practical utilizations of hybrids.

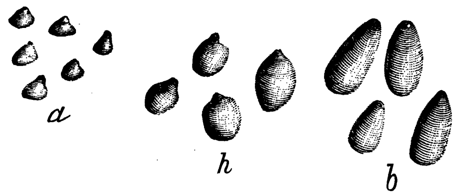

FIG. 9.—Starch grains of hybrid and parents, showing the intermediate character of hybrid: *a*, *Hedychium gardnerianum*, one parent; *h*, hybrid; *b*, *H. coronarium*, other parent. (Multiplied 500 diameters. After Macfarlane.)

As will be shown in the following pages, hybrids which were uniform and intermediate in the first generation usually vary greatly in the second and later generations, often consisting of a few forms nearly like the parents, and numerous forms representing all grades of intermediates. In some hybrids this variability is shown in the first generation. In most cases, however, such hybrids are still intermediate between the parent forms, inasmuch as they represent merely combinations of parental characters differently localized and in different proportions. Occasionally characters are shown by hybrids which can not be referred to either parent. These will be discussed later.

STERILE AND FERTILE HYBRIDS.

Hybrids arising from the union of widely different parents are very commonly sterile, often producing little or no good pollen, and sometimes, though not so often, having defective ovules and refusing to bear seed even when pollinated from one of the parent species. On the other hand, the offspring of two closely allied parents is usually fertile, often more so than the normal offspring. Formerly it was supposed that all hybrids between distinct species were sterile, but this is by no means always the case. Very frequently they are fertile with their own pollen and still more frequently with that of either parent species. The bearing of sterility on the practical utilization of hybrids in plant breeding is discussed on pages 408 and 409.

DIFFERENCE BETWEEN FIRST AND LATER GENERATIONS OF HYBRIDS.

The distinction between the first and second generations, when the hybrid is fertile, is often very marked, and this must be constantly kept in mind in order to have a clear understanding of the nature of hybrids and to be able to utilize them to the fullest extent possible in plant breeding. The first generation of the hybrid is constituted by the plants grown from the seeds produced by the cross-pollinated flower, and in very many instances, though not all, the different individuals are nearly uniform and approximately intermediate in character between the parents. Naudin, one of the most careful and trustworthy writers on plant hybrids, says: "I have always found in the hybrids which I have obtained myself and of which the origin was well known to me, a great uniformity of aspect among the individuals of the first generation coming from the same cross, no matter how many of them there were." Naegeli, however, who is an equally good authority, says: "The hybrids of varieties are especially liable to variation. When one variety is fertilized with another the descendants are often so various and so rich in forms that no plant is exactly like another." This apparent contradiction is explained by the fact that Naudin hybridized almost exclusively clearly marked species, while in the paragraph quoted Naegeli referred to offspring of two varieties or races of one species, and considers their behavior different from that of specific hybrids. Naegeli says further that "in general the hybrids in the first generation vary the less the more distantly related the parent forms are, that is, the specific hybrids vary less than the varietal hybrids, the former often being characterized by great uniformity, the latter by great diversity of form." If these hybrids of the first generation be self-pollinated or crossed among each other the progeny resulting constitutes the second generation.

Hybrids between widely different parents, when fertile, usually yield descendants showing very great diversity of character, or, as expressed by Naegeli, "the variability in the second and succeeding generations is the greater the more completely it was wanting in the first generation." Whenever, then, we cross widely diverse plants and obtain hybrids intermediate in character and all nearly alike in the first generation, we may expect these hybrids, if fertile, and self-pollinated or crossed among each other, to yield descendants showing great diversity of character. This principle is of great importance in the practice of plant breeding, as will be more fully shown later. Should the first generation not yield the desired new forms or combinations of parental characters, the possibilities are by no means exhausted, but it is quite possible that the descendants of these hybrids will yield valuable sorts. Sometimes the most extreme diversity of character does not appear until the third or even later generations of the hybrid, but often the hybrid plants in the third generation are much like the particular forms of the second generation, from which they descended.

To bring out more clearly the behavior of hybrids in successive generations, their grouping on this basis has been attempted below. The aim has been to select examples under the different categories as well authenticated as possible and clearly illustrating the point under discussion, but here, as elsewhere, no attempt whatever has been made to enumerate all hybrids which are referable to the several groups.

GROUPING OF HYBRIDS ACCORDING TO AMOUNT AND NATURE AND THE TIME OF APPEARANCE OF RESEMBLANCES TO PARENTS.

GROUP *Fertile hybrids, uniform and intermediate the first generation, but very diverse in the second and later generations, often showing both parental forms and very many grades of intermediates.*

This is certainly the most common type of hybrids between species not very closely related, but is rarer when two closely related varieties or races of one species are crossed. The following example is given by Naudin: Closely related tropical species of thorn apple (*Datura metel* and *D. meteloides*) were crossed and the first generation consisted of three plants, all alike and approximately intermediate, possibly resembling the mother species (*D. metel*) more than the father (*D. meteloides*). In the second generation the uniformity observed in the first generation was entirely wanting. Of forty-two plants, twelve were exactly like the original mother species; twenty-eight were intermediates, showing various proportions of the parent characteristics, and consequently not resembling each other; and two resembled exactly the original paternal species.

In the third generation hybrids are often still more variable than in the second generation, as, for example, according to Naudin, *Nicotiana rustica*, when fertilized by *N. paniculata*, yielded uniform and intermediate plants the first generation, and twelve plants in the second generation, very different from each other, which gave in the third generation (grown from five lots of seed taken from five of the most diverse plants of the second generation) "all the variations observed in the second generation and many new ones." Furthermore, the five lots considered separately were not more uniform than all taken together. Seeds collected from one plant produced very tall and very short individuals, some having broad and some narrow leaves, either smooth or velvety or crinkled or even; some of the plants had long-tubed and some short-tubed flowers, which were more or less sterile or absolutely sterile; some matured almost all their fruit and others did not mature any, and so on. It is a fact worthy of notice that in almost every case the most fertile plants were those most like *Nicotiana rustica*, those having long-tubed flowers, resembling the original hybrids of the first generation, being either entirely sterile or but very slightly fertile.

GROUP 2.—*Fertile hybrids which are strictly intermediate between the parents, not only in the first, but also in succeeding generations.*

Such hybrids as these, capable of propagating true to seed and not showing great variability in the second generation, are rare. Darwin states that Dr. Herbert showed him "a hybrid from two species of Loasa which, from its first production, had kept constant during several generations." Another very interesting example is the hybrid berry "Primus" (Pl. XVIII, fig. 3), derived from the Western dewberry (*Rubus ursinus*) crossed with the Siberian raspberry (*R. cratægifolis*).

This particular plant was the only fertile one among all the hybrid seedlings of the cross. Of this berry Burbank says: "None of its seedlings for any tested number of generations ever revert to the character of its parents on either side." Possibly hybrids propagating true to seed often occur when very nearly identical races of cultivated species are crossed; even then, however, variations may be very numerous the second generation, but difficult to detect, because occurring entirely within the range between the only slightly differing parents.

GROUP 3.—*Sterile intermediate, more or less uniform hybrids.*

Sterile hybrids are very commonly the result of a union of widely different parents, being very rarely produced by crossing closely related forms. It is interesting to note that the first hybrid plant of which we have any record, a cross between a carnation (*Dianthus caryophyllus*) and a sweet william (*D. barbatus*), produced by the gardener, Thomas Fairchild, in London, at the beginning of the eighteenth century, was nearly sterile. However, it proved to be a valuable sort and was propagated by cuttings for more than a hundred years.

Koelreuter, the first careful observer of plant hybrids, produced many hybrids that were sterile. For instance, a hybrid of *Nicotiana paniculata* and *N. glutinosa*, intermediate in many characters, was absolutely sterile. Luther Burbank recently produced an interesting sterile hybrid between the raspberry and strawberry. Of this he says: "Out of seven or eight hundred of these curious hybrids, not one has ever produced a berry, though blooming with the greatest profusion, and as the blooms fade a bunch resembling a miniature strawberry forms, but never matures. The hybrids when young are practically strawberry plants, but with age produce canes 5 or 6 feet high, multiplying by curious underground stolons. The leaves are invariably trifoliate and the canes are thornless or nearly so."

Focke says that "the commonest consequence of hybrid fertilization is the imperfect formation of the pollen grains in the hybrid plants. Often the anthers of the hybrid are empty, containing no pollen at all, or they are small and do not open." All students of hybrid plants agree that the pollen is much more likely to be imperfect than the ovules, and in some cases where the pollen is worthless the ovary is capable of maturing seeds if fertilized with pollen from the parent species. Some hybrids show sterility by producing no flowers. This is said by Focke to be the case with certain hybrids of Rhododendrons, Cereus, and Hymenocaulis. This is rare, however, and very many hybrid plants are characterized by excessive rather than by diminished flowering.

A remarkable case of a nearly sterile hybrid, which even when fertilized by the parent form yielded seed but rarely, and then in very small numbers, but which nevertheless was bred into a perfectly fertile variety propagated only by seed, is furnished by the so-called *Ægilops speltæformis*, a wheat-like hybrid obtained by pollinating *A. triticoides* with wheat. *A. triticoides* is itself a hybrid of *A. ovata*, a small grass occurring wild in southern Europe, and common wheat. The hybrid *A. triticoides* grows spontaneously in southern Europe along the edges of wheat fields. About fifty years ago Esprit Fabre grew this hybrid from a seed of *A. ovata*. It was afterwards produced artificially by many experimenters, proving conclusively that it is a hybrid of wheat and *A. ovata*. Fabre carefully hunted for seeds of this hybrid (*A. triticoides*), and finally in 1838 was successful. From this seed he grew plants which were very different from *A. triticoides*, being more wheat-like and more fertile. After several years' cultivation he obtained, furthermore, a fertile cereal still more like wheat, propagating true to seed, which he called "Ægilops wheat." The seeds of this were sent to many botanic gardens of Europe, where the plant was found to be as constant and fertile as a true species, and was named *A. speltæformis* by Jordan. Fabre's account of the origin of this cereal was doubted by many botanists, but was afterwards found to be correct. It had been grown more than forty years when Focke's work was published, and was said by him to have remained constant, except in the case of occasional specimens which varied in productiveness.

This example shows that it is sometimes possible to breed races propagated by seed from almost sterile hybrids. When hybrids are capable of being propagated by cuttings, grafts, bulbs, etc., however, it is, of course, possible to propagate absolutely sterile hybrids extensively.

GROUP 4.—*Sterile hybrids not uniformly intermediate, but variable, or at least occurring in two forms.*

The hybrids of this character are certainly very rare, but few cases being referred to in literature. They are interesting in showing that variability in the first generation may occasionally occur in the offspring of species so distinct as to yield sterile hybrids, although such variability is usually found only in the highly fertile offspring of closely allied species or varieties of one species. Gaertner crossed two species of tobacco (*Nicotiana quadrivalvus* with pollen of *N. macrophylla*) and obtained hybrids of two different forms, the flowers and long, narrow leaves of the commonest form resembling the mother, while the character of the flowers and leaves of the rarer form was more like the father species. This hybrid was found to be completely sterile.

Another even more remarkable case is that of certain hybrid foxgloves. Koelreuter, Gaertner, and Focke observed that the hybrids of *Digitalis purpurea* crossed with *D. lutea* produced, in addition to a more or less constant intermediate form, a number of forms very different in appearance. Focke observed among the hybrids which grew spontaneously from a cross-fertilized capsule that he had neglected to harvest when ripe, a number of aberrant forms, the most remarkable of them resembling in all particulars a different species (*Digitalis tubiflorum*). All artificially produced hybrids of these two species have been found to be completely sterile to the pollen of the parent species. The hybrids also occur in nature, in which case they are said to sometimes bear seed.

GROUP 5.—*Fertile hybrids or mongrels not uniformly intermediate in the first generation, but often reverting in this generation more or less completely to the parent forms and showing all grades of intermediates.*

Hybrids belonging to this group are almost always the offspring of two closely related species. It is, in fact, difficult to find examples of hybrids between very distinct species which in the first generation revert more or less completely to both parents, and at the same time exhibit in much the larger number of the offspring numerous grades of intermingling. This is, however, a very common phenomenon among the offspring of cultivated races of the same species, even when so different as to present to the eye very little similarity. This difference in the character of the offspring resulting from a cross between species as compared with a cross between races of cultivated plants, is very striking and very important. Gaertner, who is said to have made no less than ten thousand crosses, was so impressed by this fact that he stated it as a principle, that hybrids between different species were uniform in the first generation, while mongrels, produced by the crossing of varieties, varied greatly. Focke, the author of the most comprehensive summary of the knowledge of plant hybrids, considers this statement too broad. He says: "If one by variety means unstable garden mongrels, then this rule is valid. If one, however, means by variety constant forms of pure descent, then it is certainly untrue." Hybrid offspring of distinct species are, however, not always constant in the first generation. For instance, if the evening-blooming

Lychnis (*L. vespertina*) be crossed with the pollen of ragged robin (*L. diurna*), hybrids are produced which are very variable in the breadth of the leaves, color of the flowers, and other characteristics.

In hybrids of different species which vary in the first generation it is more common for most of the forms to resemble the one or the other parent, very few being intermediate. Darwin cites the following case: "Major Trevor Clarke crossed the little glabrous-leaved annual stock (Matthiola), with pollen of a large, red-flowered, rough-leaved biennial stock called *cocardeau* by the French, and the result was that half the seedlings had glabrous leaves and the other half rough leaves, but none had leaves in an intermediate state. That the glabrous seedlings were the product of the rough-leaved variety, and were not accidentally of the mother plant's own pollen, was shown by their tall and strong habit of growth. In the succeeding generations raised from the rough-leaved crossed seedlings some glabrous plants appeared, showing that the glabrous character, though incapable of blending with and modifying the rough leaves, was all the time latent."

Some examples of such hybrids, which were sterile, have been noted in group 4. Almost all who have worked extensively in hybridizing plants have noted the curious fact that races of cultivated plants, even though very diverse, produce very variable hybrids in the first generation, while usually by crossing wild species closely resembling each other hybrids are obtained which are constant in the first generation.

A striking case of the variability of the offspring of two crossed races of plants is furnished by Indian corn. When two sorts, differing decidedly in color or texture of the kernel, are crossed the offspring frequently varies exceedingly. Kellerman and Swingle sometimes found both parental forms and also very numerous and diverse intergrades occurring on the same ear, the kernels varying greatly in character. Sometimes, on the other hand, all the kernels on a single ear were alike or nearly so, but the different ears varied in character, the majority being intermediate between the parents, while a few bore a greater resemblance to one or the other parent, sometimes showing almost no influence from the cross.

In general, the behavior of the second and later generations of hybrids variable in the first generation is exactly analogous to that of the hybrids mentioned in group 1, that is, they tend to be still more variable than in the first generation, though they sometimes begin to come more or less true to seed in the second or third generation. It often seems as if hybrids of this group gained, as it were, one generation over those of group 1, and vary in the first instead of the second generation. It is probable that this variability in the first generation of the offspring of crosses between very closely allied races of plants is also present, but is sometimes masked, because the two parent forms are so nearly alike that the intergradations are not easily recognizable. In view of this fact, it is highly probable that in breeding plants which are to be propagated by seed it will always be necessary to practice in-and-inbreeding and selection before any new strain obtained by crossing nearly identical sorts can be relied upon to come true.

GROUP 6.—*False hybrids, resembling the one parent exclusively and showing no trace of the characteristics of the other, although often somewhat more vigorous and less fertile than normal offspring.*

It is not uncommon in hybridizing to obtain offspring resembling the maternal plant almost exactly. This has usually been attributed to the imperfect exclusion of the pollen of the mother species and consequent mixed fertilization. Naudin gave many instances where, in addition to the hybrid intermediate in character between the parents, a number were obtained exactly resembling the mother species. In one case where he crossed two thorn apples (*Datura stramonium* with pollen of *D. ceratocaula*), the capsule thus fertilized remained very small and produced but few seeds, of which many were imperfect and almost all failed to germinate the next spring. Of about sixty apparently good seeds, only three grew, and from these two plants were grown to maturity. These plants were exactly like the mother plant, but were nevertheless abnormal, because of their unusual height, being nearly twice that of the mother species, and also in dropping all the flowers produced in the lower forks. Such increased vigor and partial sterility were observed by Naudin in all intermediate hybrids of Datura, but in this case the plant resulting from the cross showed no trace of the characters of the father species, and its seeds, when planted the following year, yielded the ordinary form of the mother plant.

In a remarkable series of experiments on the various species of strawberries, conducted by Millardet, he found that most species when intercrossed yielded hybrids resembling one parent or the other. Out of six species experimented upon, only two, the Chilian and Virginian strawberries, yielded intermediate offspring when crossed. In some cases the reversion was principally to the paternal type, proving beyond question that the false hybrids resulted from a true process of fertilization, and not from any accidental access of pollen of the mother species to the crossed flowers, which was practically precluded by the careful manner in which Millardet conducted his experiments. His hybrid No. 11, grown in 1884, was obtained by crossing the White Four-Season strawberry (a white-fruited cultivated form of *Fragaria vesca*) with pollen of the "Chili velu" (a cultivated form of *F. chiloensis*). From this cross four hybrids were obtained, "of which one exactly resembled the mother species, except that the fruits were red [probably a case of reversion], while three others reproduced exactly the type of the paternal species, from which it was almost impossible to distinguish them. The three plants resembled each other very closely. All three were moderately fertile." Two of these hybrids were crossed and yielded in a second generation three plants, which were like the paternal species, *F. chiloensis*. In most cases, however, Millardet found that false hybrids resembled the mother species exclusively and that their seed when planted also reproduced the mother species true in the great majority of cases.

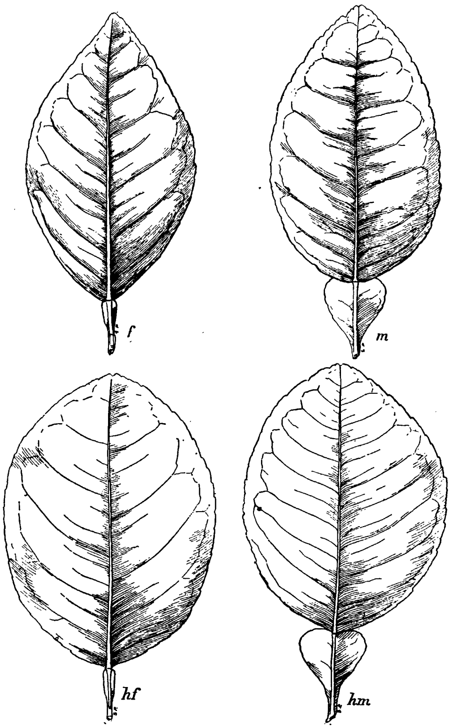

FIG. 10.—Leaves of orange and pomelo and of their hybrids of the first generation, showing close resemblance to one or the other parent: *f*, St. Michael Blood (*Citrus aurantium*), female parent; *m*, Bowen pomelo (*C. decumana*), male parent; *hf*, hybrid, resembling female parent; *hm*, hybrid, resembling male parent. (About two-fifths natural size.)

In experiments in crossing citrus fruits, carried on in Florida during the last few years, the writers have observed among the hybrids of the common orange (*Citrus aurantium*) and the pomelo (*C. decumana*) and those of the common orange and the Japanese orange (*C. nobilis*) a marked tendency to resemble the one parent to the exclusion of the other. In almost all cases, however, some of the offspring resembled one parent and some the other, in this differing somewhat from the results of Millardet with strawberries, in which in many instances he found all the hybrids to resemble the mother species. An example of these apparently false hybrids is shown by fig. 10, where *f* represents the leaf of the parent orange; *m*, the leaf of the pomelo which furnished the pollen; *hf*, leaf of one of the hybrids which resembles the mother species almost exactly; and *hm*, leaf of the hybrid which resembles the father species. It is of course probable that these apparently false hybrids may show traces of the other parent in the fruit when produced, although as yet none are evident in the foliage.

It may be readily surmised that this group of hybrids, if they can be called hybrids, are not as a rule very promising to the practical plant breeder. It is, however, highly probable that even the hybrid forms of this character which resemble the one or the other parent exclusively will be more likely to yield valuable variations than those propagated in the normal way. For instance, Millardet found in some of his false hybrids of strawberries referred to above, especially when *Fragaria elatior* was used as the seed-bearing parent, that many of the descendants, otherwise like the mother species, differed in bearing perfect flowers instead of having male and female flowers on different plants.

DESCENDANTS OF HYBRIDS.

In the preceding pages all references to the second and subsequent generations of hybrids are exclusively to plants fertilized with their own pollen or with the pollen of other hybrids of the same origin. It frequently happens, however, that hybrids are very easily fertilized

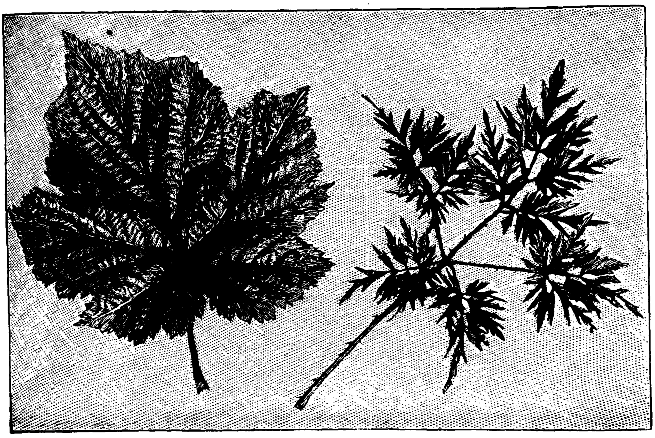

FIG. 11.—Leaves from the hybrid progeny of blackberry, showing the variations sometimes produced in second or third generation when different species have been crossed. (After Burbank.)

by one of the parental species, giving three-fourths hybrids, that is, hybrids deriving three-fourths of their characters from one form and one-fourth from the other. The wheat-like hybrid *Ægilops speltæformis*, described on page 394, is of this character, as are also many of the hybrids of the European and American grapes recently originated in France. Ganzin produced la Clairette Dorée by first fertilizing Aramon, a race of *Vitis vinifera*, with the pollen of an American species, *V. rupestris*, which is resistant to Phylloxera. One of these hybrids was crossed with the European vine, this time Grosse Clairette being the father. The resulting cross yielded the Golden Clairette, a valuable new sort, apparently highly resistant to Phylloxera. Although only two species of grapes were crossed to produce this, it being three-fourths *V. vinifera* and one-fourth *V. rupestris*, three races, or so-called varieties, were united, making it a triracial hybrid.

Frequently plant breeders cross hybrids with a species different from either of the parents, in this way obtaining trispecific hybrids. Many grape hybrids are of this nature. By crossing two hybrids having different parentage quadrispecific or quadriracial hybrids are obtained. Wichura even obtained hybrid willows combining no less than six species.

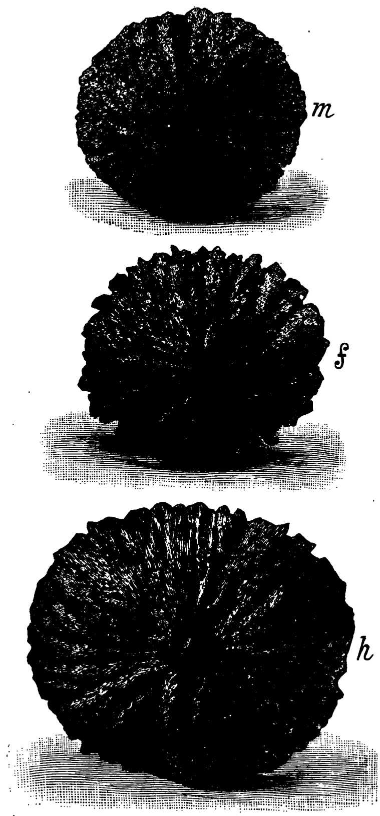

FIG. 12.—Hybrid walnut and parents: *m*, Californian black walnut (*Juglans californica*), male parent; *f*, Eastern black walnut (*J. nigra*), female parent; *h*, hybrid. (Natural size. After Burbank.)

From the very careful studies of Wittrock it appears that many pansies are complex hybrids, combining four species, and some few sorts are combinations of no less than six distinct species. Even this, however, does not fully indicate their complexity, since some of the constituent species comprise several different varieties which have also entered into the parentage of the modern pansy. Moreover, these numerous parental forms from spontaneous and artificial crossing have been combined in every conceivable proportion by pansy fanciers. Such complex hybrids are often of great value to the plant breeder and will undoubtedly be produced in constantly increasing numbers as the art of plant breeding becomes more highly developed. They are most valuable in plants which can be propagated by cuttings or grafts, since they often vary exceedingly when propagated from seed.

ATAVISTIC AND NEW CHARACTERS IN HYBRIDS.

In the preceding pages we have considered the time of appearance of resemblances to the parent species, whether in the first or later generations of the hybrid. Combinations of parental characteristics in all possible ratios have been shown to occur in the second generation of most hybrids which are fertile, and to occur often in the first generation of offspring resulting from crossing closely related races of cultivated plants. The multitudinous variations thus produced are sometimes of great worth, but are merely new combinations of characters already existing in the parent plants. There is evidence, however, that sometimes hybrids or their offspring present characters presumably belonging to remote ancestors (atavistic), or entirely new characteristics not referable to any progenitor. A striking instance of atavism is reported by Saunders, who says: "In a cross between Red Fife, male, and an Indian wheat known as Spiti Valley, female, both beardless, several distinctly bearded sorts were produced in the second generation." Now, it is highly probable that all wheats were originally bearded, as are still many of the sorts and most of the cereals belonging to related genera. Moreover, Pickering gives a bearded ear as the oldest Egyptian hieroglyphic for wheat. In the above instance, therefore, the hybrids of the second generation probably reverted in part to remote ancestral characters not present in either parent. Of course, the partial or complete reversion to the characters of grand-parental species in the second generation has already been shown to be characteristic of most hybrids resulting from a union of two clearly distinct species.

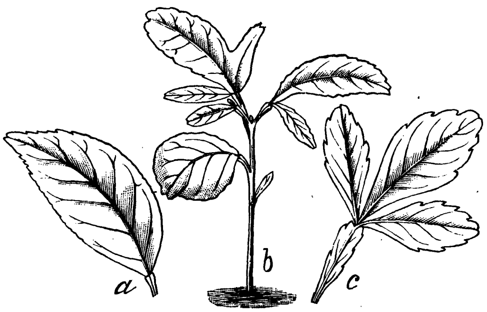

FIG. 13.—Hybrids of hardy trifoliate orange and common sweet orange: *a*, leaf resembling common orange; *b*, seedling distinctly intermediate in character; *c*, leaf resembling trifoliate orange.

The appearance of new characters, or at any rate of characters developed far more than in either parent, is not uncommon among hybrid plants, as will be discussed more fully later on. Slightly greater size and vigor are so common as to constitute the rule, as will be shown below.

PREPONDERANCE OF ONE SPECIES IN DETERMINING CHARACTER.

One parent species, whether the one bearing the seeds or the one furnishing the pollen, often outweighs the other in determining the character of the hybrid. Gaertner and Focke found in almost all cases that the hybrids of the foxgloves *Digitalis lutea* and *D. purpurea* were more nearly like *D. lutea* in every respect than *D. purpurea*, no matter which was used as the seed-bearing plant. Perhaps the best example of this preponderance of some species over others is furnished by Naudin's hybrids of *Nicotiana langsdorffii*, *N. persica*, and *N. commutata*. The last species is very nearly intermediate between the two first named, but is not identical with the hybrid which Naudin made between them. Now, *N. persica* and *N. commutata* were crossed reciprocally, yielding in both cases practically identical hybrids, all of which were very uniform and resembled *N. persica* decidedly more than *N. commutata*. *N. langsdorffii* was also crossed reciprocally with *N. commutata*, and, as with the hybrids just mentioned, the offspring in both cases showed a preponderating influence of *N. langsdorffii*, no matter whether it bore the seeds or furnished the pollen. *N. langsdorffii* and *N. persica* when crossed yielded hybrids resembling the former in their wide-spreading branches, but were very strictly intermediate in other characters. All these hybrids were perfectly fertile. It would seem that *N. persica* and *N. langsdorffii* were much more potent in controlling the characters of the hybrid offspring than *N. commutata*.

It is often assumed that when wild species are hybridized with cultivated races of plants the influence of the former preponderates in the characters of the hybrid. On the other hand, Lynch reports a hybrid of Senecio "between *Senecio multiflorus* (female) and several colour forms of the 'cultivated Cineraria'" where a "predominating influence of the 'cultivated Cineraria' in this and also in the reverse cross upon the colour and size of the flower heads was observed."

In plant breeding it will doubtless often be necessary to make successive crosses of the hybrid with the one parental form which is largely obliterated by the preponderating influence of the other in order to obtain the desired combination of characters.

DIFFERENCE BETWEEN RECIPROCAL HYBRIDS.

Two hybrids from the same parents, the father species of the one being the mother species of the other, are known as reciprocal hybrids. In the majority of cases there is no constant difference between the hybrids resulting from reciprocal crossing. Naudin found repeatedly that they could be distinguished only by the labels. There are, however, some instances given by competent authorities where such hybrids do present differences. Probably the best-authenticated case of this kind is that of certain hybrid foxgloves. Gaertner found, for instance, decided differences between reciprocal hybrids of *Digitalis ambigua* and *D. lanata*, the flowers resembling those of the mother species more closely in each case. Focke noted that *D. purpurea* fertilized with pollen of *D. lutea* gave offspring invariably having more highly colored flowers than the reverse hybrid.

Caspary found that the water lilies *Nymphœa rubra* and *N. dentata* when crossed gave offspring which in each case more closely resembled the mother species in the shape of the first few leaves, though the later leaves were alike in both hybrids.

Millardet, who has originated and studied thousands of grape hybrids, states that it appears that the paternal species preponderates in most hybrids of the grape, but that this has not been studied sufficiently to render it certain except in crossing the European vine with the American *Vitis rupestris*. He says further that "the hybrids of Aramon (or any other European sort) obtained by fertilizing it with Rupestris * * * resemble Rupestris much more than Aramon." The reciprocal hybrid, on the contrary, resembles Aramon more than it does Rupestris. In the first case the hybrids may almost if not wholly equal the father species in resistance to Phylloxera, but are inferior in prolificness, in the size of the bunches, and in the size and quality of the berries. The reciprocal hybrid has very little resistance to Phylloxera, but in fecundity, size of the bunches, and size and quality of the berries, leaves very little to be desired. Sometimes two species can be crossed only in one way, as, for example, the four-o'clocks *Mirabilis jalapa* and *M. longiflora* yield offspring only when the former is pollinated with the latter.

It is, of course, clear that no conclusions as to the relative influence of the mother and father in the production of a hybrid can be drawn unless both hybrids are produced. Many supposed rules as to the part played by the male and female elements, respectively, in determining the character of the offspring are false, having resulted from the observance of hybrids where the one or the other species was prepotent, and would have been so whether bearing the seed or furnishing the pollen.

As a rule, plant breeders can expect but little from reciprocal crossing, but when the desired form can not be obtained by the first cross a reverse order should be tried. Species which refuse to hybridize in one direction may sometimes yield offspring when the plants are reversed.

PREPOTENCY OF THE POLLEN FROM ONE PLANT OVER THAT FROM ANOTHER.

It has been observed by nearly all plant hybridizers that where two kinds of pollen are applied simultaneously to the pistil, the character of the offspring often shows that only one kind was effective in producing fecundation; in other words, one kind of pollen was prepotent. Prepotency of pollen is probably due to the greater speed with which fecundation is accomplished, that is, to there being a shorter interval of time between pollination and fecundation with pollen of the one plant than with that of the other. Gaertner crossed two species of tobacco, *N. rustica* with pollen of *N. paniculata*, and after one hour, one and a half hours, and two hours applied pollen of *N. rustica* (the mother species) to the same pistils, already dusted with pollen of *N. paniculata*. In the first case, repollinated after one hour, the fairly well-filled capsules contained seeds which produced only the pure mother species; in the second case, repollinated after one and a half hours, the imperfectly formed capsule contained seeds most of which produced the pure mother species, but also two or three hybrids; and in the third case, repollinated after two hours, the very imperfect capsules contained but few germinable seeds. all of which produced hybrids.

A more remarkable case is reported by Darwin, who says:

> The stigmas on two lately expanded flowers on a variety of cabbage called Ragged Jack, were well covered with pollen from the same plant. After an interval of twenty-three hours pollen from the Early Barnes cabbage growing at a distance was placed on both stigmas, and as the plant was left uncovered pollen from other flowers on the Ragged Jack would certainly have been left by the bees during the next two or three days on the same two stigmas. Under these circumstances, it seemed very unlikely that the pollen of the Barnes cabbage would produce any effect; but three out of the fifteen plants raised from the capsules thus produced were plainly mongrelized, and I have no doubt that the twelve other plants were affected, for they grew much more vigorously than the self-fertilized seedlings from the Ragged Jack planted at the same time and under the same conditions.

As a rule, a plant's own pollen is prepotent over that of a different species, and consequently in hybridizing it is necessary to castrate the flower in the bud to prevent self-pollination. Even if the pollen of the form used in crossing were prepotent over the plant's own pollen, it would still be necessary to prevent self-pollination, since it might have occurred long enough before the foreign pollen was applied to have had time to produce fecundation.

INCREASED VIGOR OF HYBRIDS AND CROSS-BRED PLANTS.

That unusual vigor of the offspring results from crossing slightly diverse plants has been thoroughly proved by the striking researches of Darwin and others. It has been said by Naegeli that "the consequences of fertilization reach their optimum when a certain mean difference in the origin of the sexual cells is attained," and by Fritz Müller that "every plant requires, for the production of the strongest possible and most prolific progeny, a certain amount of difference between male and female elements which unite. Fertility is diminished as well when this degree is too low (in relatives too closely related) as when it is too high (in those too little related)." Darwin says, "The offspring from the union of distinct individuals, especially if their progenitors have been subjected to very different conditions, have an immense advantage in height, weight, constitutional vigor, and fertility over the self-fertilized offspring from one of the same parents."

Attention has been called by Willis to three factors in the gain resulting from cross-fertilization, viz: *a*, fertility of mother plant; *b*, vigor of offspring, and *c*, fertility of offspring. The relative value of these factors varies with different plants. In the carnation, for instance, factor *a* of cross-fertilized plants was 9 per cent greater than in self-fertilized plants, *b* was 16 per cent greater, and *c* was 54 per cent greater; in tobacco, factor *a* was 33 per cent less than in self-fertilized plants, but factor *b* was 28 per cent greater and factor *c* 3 per cent greater. Even when the fertility of the mother plant is greatly reduced by hybridizing with a distinct species and the hybrids themselves are sterile or very infertile they nevertheless often show extraordinary vigor, that is, *b* is often greater in hybrids than in pure-bred plants, but factors *a* and *c* are usually less. In plant breeding the importance of this increased vigor is very great, and the subject will be taken up later in this paper.

DIRECT ACTION OF FOREIGN POLLEN ON PARTS OF THE MOTHER PLANT.

This phenomenon, called xenia by Focke, is one of the most remarkable observed in plant hybridization, and is considered by many as not yet proved. In some cases, however, the evidence is so extensive and so complete that it is scarcely possible to doubt that this effect does occasionally occur. The best proved instance of the immediate action of pollen is that of Indian corn. As early as 1724, Dudley said that "*Indian Corn* is of several Colours, as blue, red, and yellow; and if they are planted separately, or by themselves, so that no other Sort be near them, they will keep to their own Colour, i. e., the blue will produce blue, the white, white, &c. But if in the same Field you plant blue Corn in one Row of Hills (as we term them) and the white, or yellow, in the next Row, they will mix and interchange their Colours; that is some of the Ears of Corn in the blue Corn Rows shall be white or yellow; and some in the white or yellow Rows shall be of a blue Colour." In 1816, Dr. Savi, according to Darwin, "sowed yellow and black-seeded maize together, and on the same ears some of the grains were yellow, some black, and some mottled, the differently colored seeds being arranged in rows or irregularly."

The most convincing series of experiments was carried out by the famous French plant breeder, Henry L. de Vilmorin, in 1866. In the spring of that year he planted a dozen varieties of maize from 1,000 to 1,300 feet apart, which distance was found sufficient to prevent spontaneous intercrossing by wind-blown pollen. The ears to be crossed were enveloped in thin flannel, which excluded pollen perfectly, for such ears, if not artificially pollinated, never gave a single kernel. To have a standard for comparison, an inclosed ear of each sort was artificially pollinated from the same sort. The ears thus obtained were imperfectly filled, but the kernels reproduced all the characters of the seed planted. On the other hand, when inclosed ears were artificially crossed "with pollen from another sort * * * * the ears often but not always contained kernels showing the characteristics of their male parent. The proportion of such grains when they existed was very inconstant, being liable to vary from 1 to 60 per cent." The effect was limited to changes in the color of the kernels. In most cases the pollen of a black corn was used in crossing, and this color exists in the substance of the kernel. No conclusions were drawn except from plats of maize, the ears of which, when left exposed or fertilized with their own pollen, reproduced without change the sort planted.

In 1867 Hildebrand reported an experiment in crossing corn, using a yellow sort for the female and a dark-brown sort for the male. Realizing that the older experiments had been faulty, since no proof was given that the sort used as the female parent was pure and might not be showing the effect of a previous cross, he pollinated some of the plants of the yellow sort with their own pollen and obtained ears "all the kernels of which were exactly like the mother grains." On the other hand, two ears obtained by fertilizing the yellow sort with pollen of the dark-brown sort "had about half the kernels like those of the mother sort, or a little lighter, while the other half, scattered about among them, were a dirty violet color. On these latter, therefore, the pollen of the brown-kerneled sort had exercised a direct transforming influence."

Very many experimenters in the United States have reported instances of the immediate influence of foreign pollen on the kernels. Sturtevant observed this action at the New York Experiment Station in 1883, and Burrill reported instances of such current influence in 1887, Tracy in 1887, Kellerman and Swingle in 1888, and Hays in 1889. In 1892 McCluer published an account of his experiments and two good photographic plates showing the results. Fig. 2 of Pl. XX is taken from one of these plates, and shows the extraordinary effect that Black Mexican sweet corn (*m*) exerted on the kernels of a white dent variety (*h*), although in shape and size the ear resembled the mother sort exactly (compare *h* with *f*).

In spite of the fact that no proof is given in any of the American works that the sorts planted were free from the influence of possible crossing of previous years, yet in the light of the experiments of Vilmorin and Hildebrand, which were especially planned to exclude this source of error, we can not doubt in the majority of cases where a modification of the kernels on the female plant was due to the appearance of features characteristic of the sort which furnished the pollen, that this effect was really due to immediate action of foreign pollen and was not the result of some previous cross. This effect does not, by any means, always occur, but is more marked in some races (as sweet corn and pop corn) than in others (as flint corn).

The immediate effect of foreign pollen on the color of the seed coats of peas was observed as early as 1729, and repeatedly since then, being reported by such experimenters as Gaertner and Berkeley. Laxton observed not only an effect of the foreign pollen on the color of the seed coats, but also on the pod in some instances. His observations were confirmed by Darwin, so far as the change in color of the seed coats was concerned.

Giltay recently published very satisfactory evidence of the immediate effect of foreign pollen on the color of the kernels of rye. There are many cases on record of supposed action of foreign pollen on fruits or other parts of the mother plant far removed from the developing embryo, and though it is possible that such action occurs in some cases, most of the evidence is faulty in that there is a possibility of the effect observed being due to a previous cross or to spontaneous variation or "sporting." These curious effects of foreign pollen, though of the greatest interest to the student of heredity, are not as yet known to be of any great practical importance.

GRAFT HYBRIDS.

The evidence of the existence of graft hybrids, though becoming stronger every year, can hardly be said as yet to be conclusive. The ability of scions of certain variegated plants to communicate their variegation to the stock on which they are grafted, however, has been established by numerous observations, some made as early as 1700 by Wats, but especially by the careful experiments of Morren and Lindemuth. Variegation is, however, by some believed to be a disease which in some manner spreads through the tissues of the stock. In regard to graft hybrids Darwin says:

> The most reliable instances known to me of the formation of graft hybrids is one recorded by Mr. Poynter, who assures me, in a letter, of the entire accuracy of the statement. *Rosa devoniensis* had been budded some years previous on a white Banksian rose; and from the much enlarged point of junction, whence the Devoniensis and Banksian still continued to grow, a third branch issued which was neither pure Banksian nor pure Devoniensis, but partook of the character of both.

Recently Daniel published records of many experiments tending to show that in the cabbage family there may occur an effect of the stock on the scion to such an extent that the seeds formed by the scion will produce plants intermediate in character between the two plants united. For example, he grafted flower shoots of the tender kohl-rabi on a hardy cabbage, hoping to secure a hardy sort of kohl-rabi. The seeds produced by self-pollination (the kohl-rabi flowers having been bagged to exclude insects) yielded plants differing in aspect from the mother sort of kohl-rabi and resembling somewhat the cabbage used for stock. Still they had swollen stems useful for forage, were very hardy, and yielded from four to five times as much fodder as other sorts of cabbages able to stand the same degree of cold.

In consideration of Daniel's remarkable results the study of graft hybrids should be renewed, since the value of such hybrids in practice would be considerable could they be produced with certainty.

PRACTICAL UTILIZATION OF HYBRIDS IN PLANT BREEDING.

While very many of the best sorts of our cultivated plants have been produced by careful hybridization, yet it must be admitted that a surprisingly large number of our fruits have been produced in other ways, or at least are not known to be of hybrid origin. However, many of the chance and select seedlings, as they are termed, although not known to be of hybrid origin, are doubtless second and later generations of hybrids. Valuable hybrids are occasionally produced accidentally, a fact which still more strongly emphasizes the great advance which may be expected when the skill and industry of the trained plant breeder are applied to the work of hybridization.

Judging from some of the wonderful results which have been obtained from hybridization, it would seem that almost any desired variation can be produced if a sufficient amount of time, patience, and skill is brought to bear on its production.

VARIABILITY INDUCED BY HYBRIDIZATION

In breeding plants it is necessary to secure great variability in order to have many different forms from which to select. In the first generation hybrids are commonly intermediate in character between the two parents, as shown above, but in the second and later generations they almost invariably break up, giving many combinations of the parental characters in many proportions. Crossing these hybrids with other species or races greatly increases the range of variability which may be expected, and is a feature of great importance to the plant breeder, as it gives more opportunities of securing the combination of characters desired. If a particular combination of the characters of the parents is desired, as is usually the case, it is of the greatest importance that the necessity of planting second and later generations be recognized. Burbank says: "I expect but little result from the first generation, but after that great variations often continue to appear for several generations." In the case of hybrids between very closely allied species and between different races of the same species greater variation may be expected in the first generation, as explained above, but nevertheless, in such cases also, the second and later generations may give still more variations, and should not be neglected. The canes from different individuals of the second generation of a hybrid between the blackberry and raspberry, shown on Pl. XIX, fig. 1, illustrate in a striking manner the great variation which may be expected to occur in later generations of hybrids, as do also the leaves of a hybrid blackberry shown by fig. 11.

Many plants, poor or worthless in themselves, may be of great value to the hybridizer because of ripening earlier or later, and being more hardy or better adapted to certain soils than the good sorts, since by hybridizing these with good sorts valuable new forms may be obtained.

In plants propagated by seed the variability and instability of hybrids is to some extent a disadvantage, since a hybrid seedling may show a desirable combination of characters which in the next generation will entirely disappear.

VEGETATIVE PROPAGATION IN COMPARISON WITH SEMINAL PROPAGATION.

In the practical application of hybridization in plant breeding it is important to recognize clearly the distinction between plants propagated by seed and those which may be propagated vegetatively, that is, by cuttings, buds, grafts, suckers, etc. Hybrids are notoriously unstable, and variations shown by them are in almost all cases lost or greatly modified in the next generation. In no case can they be depended upon to reproduce true to seed until tested, and therefore any desirable variation produced by hybridization in plants propagated by seed must be "fixed" or rendered hereditary through the seed, as explained in the next section, before it can be of any value. On the other hand, the process of fixation is not necessary in plants propagated vegetatively. In such plants the scions, cuttings, or suckers used in propagation are taken from the individual plant showing the desired qualities, and the new plants, being merely portions of the original seedling, retain all its characteristics. As Burbank says, "by persistently selecting the best of one chosen special type the variety can be fixed, but of course in the case of plants propagated by division this is of no consequence, as the superlatively valuable one remains constant and the others are discarded."

FIXATION OF DESIRABLE VARIATIONS.

When a hybrid possessing desirable characters is produced from plants propagated by seed it is almost invariably necessary to render these characters hereditary by careful selection and in-and-inbreeding. Darwin says:

> Florists may learn * * * that they have the power of fixing each fleeting variety of colour if they will fertilize the flowers of the desired kind with their own pollen for half a dozen generations and grow the seedlings under the same conditions. But a cross with any other individual of the same variety must be carefully prevented, as each has its own peculiar constitution. After a dozen generations of self-fertilization it is probable that the new variety would remain constant even if grown under somewhat different conditions.

When a desirable hybrid is produced, it should be fertilized with its own pollen, the seeds thus produced planted, and the seedlings selected which most perfectly show the characters which it is desired to fix, after which these selected seedlings should be inbred and a third selection made, and so on, until the desired characters are produced true in all the seedlings. In case a desirable hybrid is found to be sterile to its own pollen, it should be fertilized if possible with pollen taken from similar hybrids showing the same variation.

In the continual self-fertilization practiced in fixing variations there is doubtless much loss of vigor. In some cases this might be avoided by making numerous hybrids between several different sets of individuals of the same sort but not closely related (that is, separated by numerous seed generations), so that several unrelated hybrids, showing practically the same combination of characters, could be obtained. These hybrids could be bred together and rigidly selected each generation, until all the seedlings produced show the desired combination of characters. However, in order to avoid the greater possibility of losing the variation, it is probably best in all cases to self-fertilize, if possible, a portion of the flowers.

ADVANTAGES AND DISADVANTAGES RESULTING FROM STERILITY.

The sterility of hybrids, mentioned on page 391, is in many cases a great hindrance to their utilization in plant breeding, particularly in races propagated by seed. Even partial sterility is often a great drawback to fruit production, and may in some cases preclude the use of otherwise valuable hybrids. If the fine European sorts of grapes are hybridized with American species resistant to Phylloxera there is no difficulty, according to Millardet, in securing hybrids sufficiently resistant and which will bear fruit of the desired quality. The great difficulty in such cases is that the hybrids in most instances are partially sterile and thus not sufficiently prolific to be valuable. Reduced fertility, however, may in some cases be overcome to some extent. According to Darwin, "if even the less fertile hybrids be artificially fertilized with hybrid pollen of the same kind their fertility, notwithstanding the frequent ill effects from manipulation, sometimes decidedly increases and goes on increasing."

Partial sterility, manifested by a lessened production of seed, is sometimes not accompanied by any diminished yield of fruits, and is therefore in such cases a positive advantage if the plant can be propagated vegetatively. This is in particular true of certain table fruits, such as oranges, pineapples, etc. In some instances sterile hybrids may be produced in any desired number by making more crosses of the parent plants. In some cases sterile hybrids, propagated vegetatively, may be valuable for stocks on which to graft other sorts, as they are commonly very vigorous, a feature which is of importance here. They may also be valuable for their wood, as in the case of Burbank's walnut, described on page 411, or for foliage plants, forage plants, etc.

It must not be supposed, however, that all hybrids are in some degree sterile. In very many instances the opposite is true, the cross resulting in increased fertility. Fritz Müller found some species of Abutilon to yield capsules containing more seed when hybridized with another species than when cross-pollinated from another plant of the same species. Additional fertility may thus be expected in certain hybrids and their progeny, notwithstanding that sterility is in many cases the rule.

HYBRIDS MOST USEFUL TO THE PLANT BREEDER.

The majority of hybrids between distinct species are in the first generation intermediate between the parent species, resembling each plant in about equal degree, and in some cases there appears to be a perfect blending of the characters. Such hybrids may frequently be of use to the plant breeder in securing the amelioration of certain undesirable qualities. Valuable sorts of flowers intermediate in color and shape, and fruits intermediate in odor, flavor, texture, color, etc., may be secured in this way.

In many hybrids the individual characters of each parent remain distinct, though intimately associated, forming the so-called mosaic hybrids (p. 391). Such is the case in variegated flowers, where the color of each parent usually reappears, but in distinct blotches (Pl. XVII, fig. 3). Again, the leaf may resemble one parent and the fruit the other, and in still more extreme cases the entire top, the foliage, appearance and quality of the fruit, etc., of the hybrid may resemble one parent mainly, while in hardiness, vigor, resistance to disease, etc., it may resemble the other parent.

It is upon these large-pattern mosaic hybrids that the plant breeder must depend largely for valuable results. Many hybrids of this nature are described on the following pages; for instance, the French grape hybrids, possessing the resistance to Phylloxera of certain American grapes; the hybrid pansies, possessing the odor and perennial habit of one of the parents; the hybrid Turkish tobacco, having to a large extent the flavor and aroma of the Havana tobacco, one of the parents, etc.

The occurrence of apparently totally new characters, distinct from those of either parent, as a result of hybridization, has not been generally emphasized as a factor in plant breeding. However, some of the striking modifications obtained by plant breeders can hardly be considered other than as new characters. What new characters can be obtained can not be predicted from the parents selected for hybridizing, and while such characters can not be expected to occur commonly, yet that they do occasionally appear can not be doubted. Illustrations of such striking new characters, which show the extraordinary results that may occasionally be obtained by hybridizing, are the excessive size and rapidity of growth of Burbank's hybrid walnuts; the size and time of fruiting of the raspberry-blackberry hybrid "Primus;" the excessive increase in quinine content in the hybrid Cinchona (*C. ledgeriana*); the remarkable increase in starch content of Cimbals' potato Präsident von Juncker, etc., described in detail on pages 411, 417 and 418.

Focke announces as a general principle that "monstrous or abnormal forms of floral organs are much more common in hybrids than in individuals of pure descent," and states further that double flowers are especially frequent in hybrid plants. Such examples could be multiplied indefinitely, but enough have been cited to show that these striking new characters are of superlative interest to the plant breeder.

SOME SPECIAL FEATURES OBTAINED BY HYBRIDIZATION.

INCREASED SIZE AND VIGOR.

Hybrids between very different species are said to be often very weak when young, and also difficult to grow successfully. In some cases, however, crosses between very different species give unusually vigorous offspring. Burbidge says: "I have in several cases noted the healthy, vigorous appearance of Mr. Dominy's hybrid and bigeneric hybrid orchids compared with the parent plants." Darwin subscribes to the same view in the statements that "true hybrids raised from entirely distinct species, though they lose in fertility, often gain in size and constitutional vigour," and that "Clotzsch crossed *Pinus sylvestris* and *P. nigricans*, *Quercus robur* and *Q. pedunculata*, *Alnus glutinosa* and *A. incana*, *Ulmus campestris* and *U. effusa*, and the cross-fertilized seeds, as well as seeds of the pure parent-trees, were all sown at the same time and in the same place. The result was that after an interval of eight years the hybrids were one-third taller than the pure trees."

Burbank's numerous hybrids furnish many instances of excessive increase in vigor, size of fruit, etc., resulting from crossing distinct species. A hybrid between the English walnut (*Juglans regia*) and the Californian black walnut (*J. californica*) possesses extraordinary vigor of growth, which may render it of exceptional value as a lumber and ornamental tree. "The hybrid grows twice as fast as the combined growth of both parents. The leaves * * * are from 2 feet to a full yard in length. * * * The wood is very compact, with lustrous, silky grain, taking a beautiful polish, and as the annual layers of growth are an inch or more in thickness and the medullary rays prominent, the effect is unique." Another of Burbank's hybrid walnuts, obtained by crossing the black walnut with pollen of the Californian black walnut, produces fruit of excessive size, it being much larger than those of either parent (fig. 12).

The raspberry-blackberry hybrid "Primus," produced by crossing the Western dewberry (*Rubus ursinus*) with the Siberian raspberry (*R. cratægifolius*) is also an interesting case. In his description of this hybrid berry, Burbank says: "It is also remarkable that the hybrid should ripen its fruit several weeks before either of its parents, and excel them much in productiveness and size of fruit, though retaining the general appearance and combined flavors of both" (Pl.

XVIII, fig. 3). Slightly increased size and vigor frequently result from crossing closely related sorts and species, as we shall see later, but the excessive increase in size in the above-described walnuts and raspberry-blackberry hybrids can hardly be considered otherwise than as a new character.

From the preceding statements, it seems certain that even crosses between distinct species may frequently produce offspring of greatly increased vegetative vigor, and that this vigor may often be of the greatest consequence in the breeding of plants, enabling the hybrid to endure much better than either of the parent species the deteriorating effects of unsuitable soils or climates. A case in point is that of *Primula venzoi*, the hybrid offspring of *P. tyrolensis* and *P. wolfeniana*. According to Kerner, both parent species are difficult to rear in gardens, even when the greatest care is bestowed upon their cultivation. The hybrid *P. venzoi*, however, will flourish in extreme luxuriance if planted close to them in the same soil and under the same external conditions.

In some cases the increase in vegetative vigor secured by crossing distinct species is at the expense of fertility, but this is by no means true in all. Focke says that "it was formerly thought that the diminished sexual fruitfulness is compensated by a greater vegetative luxuriance, a statement the untenableness of which, as Gaertner showed, is most plainly demonstrated by the fact that many of the most fruitful crosses (Datura, Mirabilis) are also distinguished by a most gigantic growth." On this subject Fritz Müller also says: "So far as my experience goes, the hybrids which grow the most luxuriantly are generally the most fruitful."

From results obtained by Millardet, it would seem that in some cases the exceptional vigor due to hybridization of distinct species might be secured without a noticeable change in the species which it is desired to breed true. These are the so-called false hybrids discussed above, resembling one parent exclusively. Thus, Millardet hybridized two strawberries (*Fragaria vesca* with *F. elatior*) and obtained five very vigorous and fruitful hybrids of the *vesca* type. Seeds from these hybrids were planted and the plants of the second generation, also of the pure *vesca* type, were remarkably vigorous.

The beneficial effect of fertilizing plants with pollen of different individuals of the same species was conclusively proved by Darwin, and is now well understood. That unusual vigor frequently results from crossing plants of closely related sorts or different strains or races of the same species, and that this may be of great use in increasing the vigor and yield of many of our common cultivated plants, has not been so thoroughly realized; indeed the great economic importance of this fact has been largely overlooked. The increased vigor produced by crossing different sorts is well illustrated by Darwin's results in crossing tobacco, which is commonly self-fertilized.

He found that simple cross-fertilization with the same strain had but little effect, but when the flowers of slightly different sorts or strains were crossed the resulting seedlings showed the effect of the cross in an extraordinary degree. "This was shown in several ways—by the earlier germination of the crossed seeds, by the more rapid growth of the seedlings while quite young, by the earlier flowering of the mature plants, as well as by the greater height which they ultimately attained. The superiority of the crossed plants was shown still more plainly when the two lots were weighed, the weight of the crossed plants to that of the self-fertilized in the two crowded pots being as 100 to 37. Better evidence could hardly be desired of the immense advantage derived from a cross with a fresh stock."

In cases where there is no particular object in keeping the varieties pure, a marked increase in yield may be obtained by using crossed seed. The valuable practical results which may be secured in this way are indicated by results obtained at the Illinois Experiment Station by Morrow and Gardner in crossing various sorts of corn. Of fifteen cross-bred corns tested, twelve gave a decided increase in yield over that of the parent sorts, ranging from 2 to 86 per cent in individual cases. In three cases a decrease in yield of from 8 to 20 per cent resulted. In the fifteen cases taken together an average increase in yield of about 16 per cent was secured. In some cases the cross-bred corns were grown the second generation without crossing and showed a decidedly larger yield than the parent varieties. A number of crossing experiments of a similar nature had previously been made by McClure with corn and practically the same results obtained. "The corn grown from the crossed seed was in nearly all cases clearly increased in size as a result of crossing" (Pl. XX, fig. 1). "Nearly all the corn grown a second year from the crosses is smaller than that grown the first year, though most of it is yet larger than the average size of the parent varieties."

In the majority of cases crossing distinct sorts improves the vigor and results in greatly increased yield. By selecting varieties which give increased yields uniformly when crossed and crossing these for seed corn it seems certain that the average yield can be greatly increased. Securing seed corn from a cross of any two sorts desired is not a difficult or expensive process, being easily accomplished by planting the two desired sorts in alternate rows and removing the tassels, as soon as they appear, from the one to be used as the female parent. The ears that form on the rows from which the tassels have been removed will have been crossed with pollen from the variety from which the tassels have not been removed. The seed corn should therefore be selected from the ears produced on the detasseled rows. The field planted to the two varieties, as above described, to secure crossed seed should be somewhat isolated from other cornfields, and should be of sufficient size to produce the necessary quantity of seed.

The only extra cost incurred in producing seed corn in this way is the cost of detasseling the alternate rows, as ears will form on both as usual.

In case of fruits and plants propagated vegetatively by suckers, cuttings, grafts, etc., increased vigor obtained in this way could probably be retained indefinitely and would be of the greatest value. It is probable also, as Darwin suggests, that increased fertility and yield would be secured by obtaining seeds of the same sort grown for some time at a distance under different conditions and planting in alternate rows with home-grown seed, so that the different strains would be crossed. The increased vigor resulting from crossing closely related sorts may be of the utmost importance in aiding plants to resist disease. Knight found this to be the case with certain wheats which he obtained by crossing different sorts. He says: "In the years 1795 and 1796, when almost the whole crop of corn in the island [Great Britain] was blighted, the varieties thus obtained, and these only, escaped in this neighbourhood, though sown in several different soils and situations."

The increased vigor and fruitfulness which almost invariably result from crossing closely related sorts or varieties is a principle of the utmost importance in our common agricultural practices, for we greatly need more vigorous forage plants, timber and shade trees, vegetables, etc., and more prolific grains and fruits.

BREEDING HARDY SORTS.

Tender plants may be rendered more resistant to cold by crossing them with hardy species or races. Thus, according to Verlot, the forms of *Rhododendron arboreum* are rendered hardier by crossing with *R. catawbiense*. Macfarlane has called attention to the hardiness of a hybrid between the hardy *Montbretia pottsii* and *Tritonia aurea*, which latter is easily injured by cold. He says, referring to the winter of 1891–92: "The corms of the first [*Montbretia*] appear scarcely to have been injured. Those of the hybrid have been largely killed off, at least to the extent of 60 per cent, while Tritonia, never hardy in exposed ground, has survived only where it is planted against, and can creep along, the outer side of a hothouse wall." A second case is also described by Macfarlane where a hybrid between a hardy and a tender species is intermediate in hardiness between the two. He says: "*Philesia buxifolia* is a hardy plant and resists well our winter colds. *Lapageria rosea* requires the temperature of a cool hothouse to flourish, while the hybrid succeeds if kept protected from frost and the more cutting winds. In the southern counties of Britain it lives and flowers out of doors."

Originating hardy races of cultivated plants is a line of work of great worth, rendering it possible to cultivate valuable kinds farther north than they have been in the past, and lessening the danger from the sudden and great changes of temperature to which they are exposed in many parts of the United States.

In view of the great injury caused to orange and lemon trees in Florida, Louisiana, and California by the severe freezes which occasionally occur, it would be of immense value if good sorts of oranges and lemons which are more resistant to cold than any now existing could be produced. Fortunately, the Japanese trifoliate orange (*Citrus trifoliata*), although its fruits are small and of little value except for preserves, is deciduous and so hardy that it can be grown without protection as far north as Philadelphia. The experiments of the writers have proved that hybrids may be made successfully between this hardy species of Citrus and the good sorts of oranges and lemons commonly grown. Furthermore, some of these hybrid plants show by their irregularly trilobed leaves (fig. 13) that they are intermediate in character between the parents, and do not exhibit the overwhelming preponderance of one or the other parent shown by the hybrids of the orange and pomelo described on page 397. If these hybrids are produced in sufficient numbers we may reasonably expect to find among the many some having the desired combination of characters, that is, the hardiness of the trifoliate orange and the size and quality of fruit of the ordinary orange and lemon. Since these hybrids are difficult to produce, their seeds, if any are developed, should be planted in order to secure numerous plants of the second generation, which are not only easier to obtain, but are in general more variable and consequently more likely to yield the desired forms. The problem here is very similar to that which the French hybridizers have successfully solved in obtaining hybrid grapes combining the resistance to Phylloxera of the American grape and the quality and size of fruit of the European grape (p. 416). An increase in hardiness of plums, peaches, pears, and, indeed, of hosts of our most valuable crops, would be of immense value and could doubtless be secured by hybridization and selection.

ADAPTATION TO WARMER CLIMATES.

In the previous section, methods of obtaining hardy sorts by hybridization was discussed. With many plants it is just as important to secure sorts adapted to growth in warmer climates, making possible the southward extension of the territory in which the plant can be cultivated profitably. The Kieffer and Le Conte pears furnish excellent illustrations of valuable sorts of this kind. These pears are almost certainly hybrids between the Chinese sand pear (*Pyrus sinensis*) and the common European pear (*P. communis*), since both were grown from seeds of the sand pear obtained from trees which were surrounded by various European pears. The partial self-sterility of the sand pear and the great ease with which cross-pollination is effected by insects thus leaves but little doubt that the seeds were the result of accidental hybridization. The Chinese sand pear is cultivated mainly as an ornamental tree and for stocks on which to bud other sorts, the fruit being of very poor quality.

The adaptability of the Kieffer and Le Conte pears to growth in warmer climates is doubtless derived from the mother, the Chinese sand pear, from which parent is probably derived in part the unusual vigor and resistance to disease. On the other hand, the quality of the fruit was largely derived from the common pear.

These two hybrid sorts have practically revolutionized pear culture in the southern part of the United States, having extended the range of profitable commercial pear growing hundreds of miles southward. Waite says in regard to this: "No single element has exerted more influence on pear culture in the Eastern United States than the introduction of the oriental species of pear. The Kieffer and Le Conte have so far brought about most of the changes. From Virginia and southward to the orange region of Florida these two varieties have monopolized the pear growers' attention. In fact, they have made the Southern pear culture." Still greater improvements may be expected when extensive and carefully planned experiments can be carried out in hybridizing the oriental and European pears.

SORTS RESISTANT TO DISEASE.

It has long been known that certain races and sorts are less subject than others to some diseases, but it was only recently that this fact was brought into prominence, and is largely the result of efforts of the French vineyardists to secure grapes immune from Phylloxera, black rot, chlorosis, etc. The extensive grape industry of France was threatened with destruction by Phylloxera, an insect affecting the roots of the vine, until it was learned that certain American species, as *Vitis riparia* and *V. rupestris*, were practically immune from it. This has led to the fine European varieties being grafted extensively on these resistant stocks. A "direct producer"—that is, a variety propagated by cuttings and not budded or grafted—was thought desirable, however, and large sums were expended by the French Government and by private individuals to secure by hybridization sorts having the Phylloxera-resistant character of the American grapes and the fine fruit of the European. Several very excellent hybrids have been obtained which possess these characters, so that it is very probable that direct-producing sorts, meeting all the demands of different regions, can be secured. Millardet, who has been very active in this investigation, says: "The great difficulty is not to obtain resistance to Phylloxera and to mildew, nor even to obtain size and quality of fruit, but to secure the fertility of the plant." The relative susceptibility of the various grapes to black rot has also been studied, and it seems probable that this destructive malady may be prevented successfully by securing resistant sorts. According to Ratoin, no native French grapes are entirely immune. Jurançon Noir is the most resistant, as when surrounded by rotting grapes it did not lose a tenth of its bunches; Blanquette de Limoux is as good as Jurançon, two sprayings being sufficient to save a crop where the whole vineyard is composed of this sort; Hybrid J 503 of Couderc, a black grape, obtained by crossing *V. rupestris* and Petit Bouschet, is immune; 4401 of Couderc, a hybrid of *V. rupestris* and Chasselas rose, is very resistant, and Seibel No. 1 is also of this category. In 1888 M. Fournié sowed seed obtained by crossing *V. riparia*, *V. rupestris*, and Portugais Bleu, and secured a hybrid which is very resistant to Phylloxera and chlorosis, and seems to be entirely immune from fungous diseases. Placed among vines ravaged by black rot in Lot-et-Garonne it remained perfectly healthy without treatment. It is, moreover, a sort that yields well, forty-five bunches being counted on a single plant. Degrully reports that Couderc's hybrids of Cunningham and Folle and Cunningham and Aramon are very resistant to black rot. The almost absolute immunity of Cunningham seems to be easily communicated to its hybrids.

Chlorosis, a disease induced by planting on soils containing an excess of lime, may also be avoided by using resistant varieties. According to Roy-Cevrier, Couderc's hybrid 1202 of Mourvedre and Rupestris is very well adapted to calcareous soils and is resistant to chlorosis.

In resistance to disease very marked differences exist in certain species and races of oranges. For instance, the sour orange is practically immune from mal-di-gomma, and the disease is largely controlled by budding the sweet orange on this stock. The sour orange is also largely immune from blight, and it is probable that a blight-resistant sort of the sweet orange could be obtained by crossing with it. Again, the Drake Star, a very excellent late orange, but a shy bearer, has been found by the writers to be almost entirely immune from "rust," which is caused by a surface-feeding mite (Phytoptidæ). Other rust-resistant sorts could probably be obtained by crossing the Drake Star with other sweet oranges.

Sorts somewhat resistant to disease can be found among almost all our cultivated fruits, and from the results obtained in France with the grape it seems probable that many plant diseases could be successfully controlled by breeding resistant sorts.

INCREASED PERCENTAGE OF STARCH, SUGAR, ETC.

That very valuable improvements may be made in this direction is clearly shown by the results of Cimbals, a celebrated German plant breeder, in the improvement of the potato. "The well-known sort Magnum Bonum yields about 60 cwt. per morgen [about five-eighths of an acre], with 15 per cent starch content, that is, 9 cwt. starch, and Cimbals' new sort, 'Präsident von Juncker,' yields 140 cwt. per morgen, with 26 per cent starch content, that is, over 36 cwt. starch." Not only was an increased yield obtained in this latter case, but the per cent of starch was increased very decidedly, so that the yield of starch was four times as great—a very important feature, particularly in Germany, where potatoes for distilleries, starch factories, and other industrial purposes are sold according to starch content.

Kuntze described a remarkable Chinchona (*C. ledgeriana*) supposed to be a hybrid of *C. pavoniana* and *C. weddelliana*, which shows an extraordinarily large quinine content. It is a mosaic hybrid, having the parental characters dissociated to a considerable extent, that is, showing side by side, and the bark often contains from 5 to 13¼ per cent of quinine (13½ per cent corresponds to 17.83 per cent sulphate of quinine), or "from three to four times as much quinine as other rich barks." This hybrid is sterile and difficult to propagate, so Kuntze recommends its production by seed obtained by artificially crossing the parent species.

The sugar content of the sugar beet has been largely increased by Vilmorin, mainly by careful selection of seed. It is very probable that important results could also be obtained in the United States by hybridizing the best sorts existing. The protein content of some of our important food plants, and the camphor, rubber, and tannin content of plants cultivated for these products, could doubtless be greatly increased by hybridization and selection.

CHANGE OF SEASON AND OF DURATION OF LIFE.

Frequently the time of blooming and fruiting may be changed by hybridization, and thus the season prolonged and sorts secured which bloom or fruit at times different from the blooming or fruiting time of existing sorts, which is a feature of great practical importance in fruit and flower industries. Burbank's blackberry-raspberry hybrid "Primus," described on page 411, is an excellent illustration of this result.

In many annual and biennial plants an extension of the period of growth and of production of flowers or fruit, rendering them perennial, would be a great acquisition. This could probably be obtained in many instances without detriment to the flower or the fruit, by crossing such plants with related perennial species. "Foremost among the problems to be solved by the pansy raisers," says Wittrock, "we must place the question of making the pansy perennial instead of annual or biennial. A remarkable step in this direction has already been taken by the English and Scotch pansy growers, who, with very good results, have used the perennial *Viola cornuta* for crossing with garden pansies." The perennial habit of the tufted pansies, or violas, was derived from the English *V. lutea* and the Pyrenean *V. cornuta*, which were crossed with the garden pansies.

ACQUISITION OF ODOR.

There is evidence which shows that odorless plants have been rendered fragrant by hybridizing with scented species or varieties. According to Wittrock, pansies have been considerably improved in this respect by crossing various sorts with the fragrant *V. cornuta*. Violetta, a fragrant sort, was produced by crossing *V. cornuta* with pollen of the pansy Blue King. Sensation, another scented variety, was also produced by crossing *V. cornuta* and the pansy. Wittrock, who is probably the best authority on violets and pansies, says: "No pains have been spared of late by the pansy cultivators of Great Britain to increase the charm of the pansy by obtaining perfume as well as beauty, but by a more extensive use of the odoriferous alpine species (*V. cornuta* L. and *V. lutea* Huds., var. *grandiflora* (L.) Vill.) for hybridization doubtless much may still be done in this direction."

BETTER QUALITY AND FLAVOR.

Probably the most satisfactory method of obtaining improved and unique flavor is through the variations produced by crossing different races or species. The exceedingly valuable results which may be obtained in this way are shown by what has been accomplished in the improvement of the quality of smoking tobaccos. The various forms of Havana tobaccos, because of their superiority to all others, have been used in crossing with other varieties to improve their flavor. The most valuable results which have been obtained in this way, according to Comes, "are certain Turkish tobaccos, which unite marvelously the suavity of aroma of the Havana with the mild flavor of the Macrophylla," a mild-flavored, large-leafed tobacco. The various forms of the famous Jenidje of Drama and of Aya Soluk are cited by Comes as examples. Thus far almost no attempt has been made in America to improve the cultivated races of tobacco by hybridization. Recently very numerous and extensive experiments have been made in Florida to grow the famous Cuban Vuelta Abajo tobacco. All attempts thus far have been directed to securing from Cuba seed of the sort desired, and cultivating and curing the crop as nearly as possible in the same way as is done in Cuba. It seems probable, however, that even more valuable and far-reaching results might be obtained by infusing the quality of the Vuelta Abajo into some of the best widely cultivated native sorts by hybridization. In this way the hardiness of our native sorts might be combined with the flavor and quality of the Vuelta Abajo, thus making it possible to grow superior smoking tobacco over a widely extended area.

Many of our fruits and nuts are capable of marked improvement in the same way. The modifications in flavor and color which may be obtained, if not superior to the parent sorts may at least form interesting and valuable novelties. The Transcendent crab apple, a hybrid between the common apple and the Siberian crab apple; the Soulard and kindred crab apples; hybrids between the apple and the native west American crab apple, etc., are illustrations of valuable combinations in quality, flavor, and size obtained among fleshy fruits by hybridization. The Le Conte and Kieffer pears already referred to are also examples of this effect.

BREEDING BETTER STOCKS.

One of the most promising lines of work for the plant breeder is the origination of sorts of plants to be used exclusively for stocks. Hybrids of unusual vigor, even though absolutely sterile, may prove of great value for stocks if they are capable of being propagated vegetatively. Millardet says that some of his hybrids of the European and American vines exhibit a "degree of vigor which is simply incredible." Some of those sown in 1883 were 2 and one even 3 inches in diameter in 1889. Some of Ganzin's observations go to show that the European vine thrives better on such hybrid stocks than on the pure American species, having more affinity for the former.

The importance of breeding sorts of the vine adapted to particular soil conditions has long been recognized by the French viticulturists. Degrully called attention to some hybrids of the European grape with *Vitis berlandieri* as having great resistance to chlorosis, a disease due to excess of lime. Several of them were able to thrive in soils containing 50 to 60 per cent of lime and some few even where there was 60 to 63 per cent. Munson has done valuable work in this line in America, but much still remains to be accomplished. The Marianna plum, which is propagated extensively from cuttings to serve as stocks for other plums, is a hybrid supposedly of Mirobolan and Chickasaw plums. A very considerable increase in productiveness and extension of the area of cultivation of our most valuable fruits may be expected when stocks are bred as carefully as are at present the sorts used for grafting on them.